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Visual Imagery Subcategories and their Neural Associations

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Introduction

Visualizing is a task people do every day. Whether it involves trying to remember the details of an event or the route to a supermarket, visual imagery is an experience people use daily. Research on visual imagery, or the ability to recreate and manipulate visual representations without the presence of the corresponding visual stimuli (Ganis, 2011), typically involves participants performing a visual imagery task while their brain activity is recorded using fMRI or other brain activity-measuring technology. This allows for the associations to be made between brain areas and visual imagery.

Visual imagery research can investigate visual imagery in general or one of its subcategories. A visual imagery subcategory refers to a specific aspect of visual imagery, such as scene construction, the imagining of visual details in a scene (Rubin, 2022), or visuospatial imagery, the ability to imagine something changing visually (Dehn, 2011). While most studies stick to investigating one subcategory, some research explores two or more subcategories (Hassabis, 2007b; Dijkstra, 2017; Mast, 2003; Yu, 2016).

Research investigating visual imagery subcategories seems to be present in visual imagery meta-analyses, as they consider a variety of visual imagery research. While existing visual imagery meta-analyses are useful for understanding visual imagery, they do not focus on the different visual imagery subcategories investigated in the research pool they collect. Instead, they aim to investigate a potential network, a group of brain areas, associated with either visual imagery in general or the network of one subcategory (Winlove, 2018; Spagna, 2021; Mazard, 2004; Hétu, 2013). Therefore, this literature review aims to address this gap by compiling the brain areas associated with various visual imagery subcategories and discussing how these brain areas contribute to each subcategory.

Methodology

A systematic review was conducted to gather past research investigating visual imagery and its neural origins. Keywords and modifiers were used to search for relevant research in *Google Scholar* (see Table 1). Research conducted before the year 2000 was excluded to prevent the inclusion of any research whose findings may have been made irrelevant by future research.

This search procedure resulted in a final list of four research projects. From the resulting research, four different visual imagery subcategories and ten different brain areas were identified (see Table 2 and Table 3). There was an initial list of 19 research projects, 15 of which were cut to limit the discussion to brain areas that have the greatest involvement in visual imagery.

The brain areas that appeared most frequently in the search were recorded and intended to be discussed. These areas included those that overlap in their location, such as the hippocampus and right hippocampus. In the following section, the contributions and explanations of the brain areas' relation to the visual imagery subcategories are discussed.

Table 1.

Keywords and Modifiers

Database	**Keywords**	**Modifiers 1**	**Modifiers 2**	**Modifier 3**
Google Scholar	Neural	basis	visual	imagery
-	Neuronal	foundations	mental	-
-	-	correlates	brain	-
-	-	associations	-	-
-	-	networks	-	-
-	-	substrates	-	-

Note. This table details the database, keywords, and modifiers used for the search procedure to collect research. All possible combinations of keywords and modifiers were entered into the search bar for the database *Google Scholar*. These combinations were put in the order of keyword, modifiers 1, the word "of", modifiers 2, and modifier 3 (i.e. "Neural basis of visual imagery"). A "-" indicates a blank space on the table.

Table 2.

Positive Associations

Visual Imagery Subcategory	**Frequent Positively Associated Brain Areas**
Scene Construction	Parahippocampal Gyrus, Hippocampus, Retrosplenial Cortex, Posterior Parietal Cortex
Episodic Memory	Parahippocampal Gyrus, Right Hippocampus, Retrosplenial Cortex, Posterior Parietal Cortex, Precuneus, Posterior Cingulate Cortex
Imagery Vividness	Precuneus, Insula, Early Visual Cortex, Parahippocampal Gyrus, Hippocampus, Posterior Cingulate Cortex, Visual Association Cortex
Visuospatial Imagery	Left Inferior Parietal Cortex, Parahippocampal Gyrus, Precuneus, Posterior Cingulate Cortex

Note. This table details the most frequently appearing brain areas that were positively associated with their respective visual imagery subcategory found during the search procedure.

Table 3.

Negative Associations with the Visual Imagery Subcategories

Visual Imagery Subcategory	**Frequent Negatively Associated Brain Areas**
Imagery Vividness	Insula, Area V1, Area V2
Visuospatial Imagery	Area V1, Area V2

Note. This table details the most frequently appearing brain areas that were negatively associated with their respective visual imagery subcategories found during the search procedure. A negative association indicates that activity in these brain areas is linked to weaker visual imagery. In this case, negative associations were only found for imagery vividness and visuospatial imagery.

Results

Scene Construction

Scene construction refers to the mental process of vividly creating and detailing a specific event's context. This includes its location, sensations, and background details (Rubin, 2022). According to one experiment, scene construction appears to activate the parahippocampal gyrus, hippocampus, retrosplenial cortex, and posterior parietal cortex (Hassabis, 2007b).

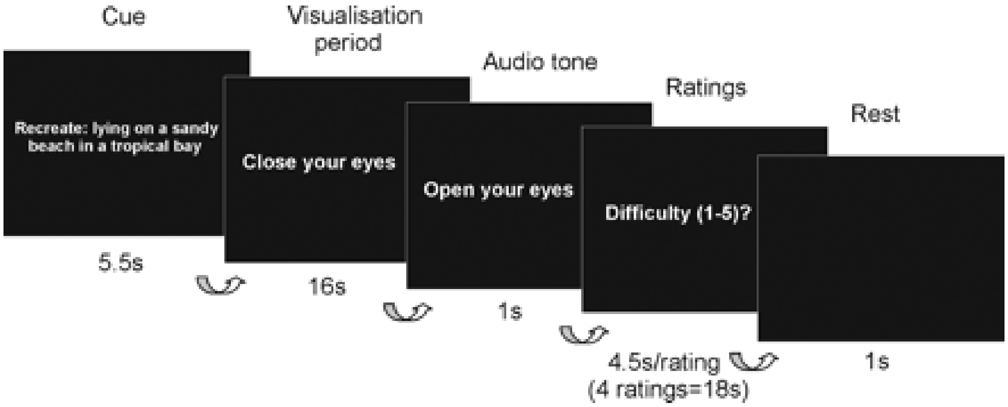
In this experiment, participants were first tasked in an interview session to generate complex spatial contexts and imagine the sensory experiences that would take place in those contexts. Participants first completed an interview session, where they were asked to imagine themselves lying on a beach and describe what they could see, hear, smell, and feel. Following this they were asked to imagine 10 real episodic memories along with the sensory experiences that accompanied them like in the previous task.

After the interview session participants were then placed into one of seven conditions: ‘real memory’(RM), ‘imagined scene’(IS), ‘new scene’(NS), ‘real objects’(RO), ‘imagined objects’(IO), ‘new object’(NO), and the low imagery baseline condition. The seven conditions can be divided further into scene conditions (RM, IS, NS), object conditions (RO, IO, NO), and the low imagery baseline condition.

In each condition, participants received a specific keyword prompt indicating the task of the condition, followed by a concise description of the object or scene they were instructed to imagine. The keyword prompts were ’recall’, ‘recreate’, ‘imagine’, and ‘focus’. ‘Recall’ was used for the RM and RO conditions. This indicated that the description that followed was either a real autobiographical memory personal to them or an object that was already presented in the interview session. ‘Recreate’ was used for the IS and IO conditions, which indicated that participants were supposed to remember an imagined scene or object created during the interview session. ‘Imagine’ was used for the NS and NO conditions, where participants were to imagine a new fictitious scene or object for the first time. ‘Focus’ was used for the low imagery baseline condition, which asked participants to imagine and then focus on a white crosshair put on a black background (see Figure 1).

Figure 1.

Hassabis et al Slides

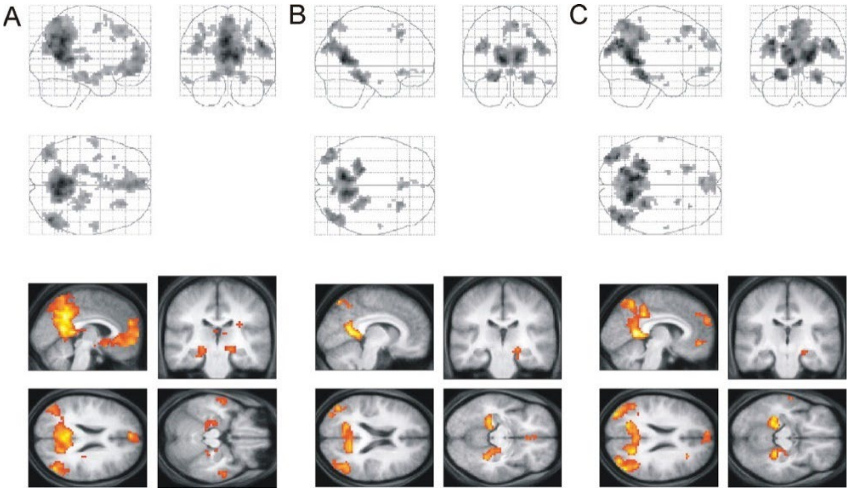


Note. These are the series of slides shown to participants, in left to right chronological order. Participants were first presented with a cue slide that indicated what they were supposed to imagine. This was followed by a slide asking them to close their eyes and imagine. After a period of time, a simple audio cue was played indicating that participants stop imagining and open their eyes. Participants then rated their just visualized scene across four different scales: difficulty, vividness, coherence, and memory. Afterward, they had a resting period before starting their next condition. From "Using Imagination to Understand the Neural Basis of Episodic Memory" by Hassabis, D., Kumaran, D., & Maguire, E. A., 2007, *The Journal of Neuroscience*, *27*(52), 14365-14374 (https://doi.org/10.1523/JNEUROSCI.4549-07.2007) Copyright 2007 by the Society for Neuroscience

This study measured brain activity using fMRI while the participants imagined the prompt. The results established the networks associated with episodic memory, newly imagined fictitious scenes, and previously imagined fictitious scenes (see Figure 2).

Figure 2.

Hassabis et al Networks

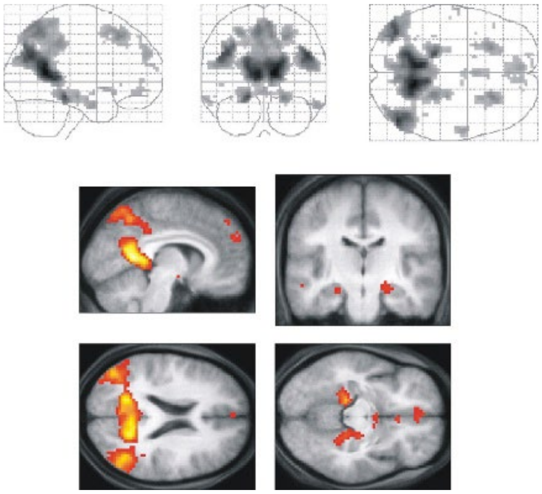


Note. This image illustrates various networks that result from the comparisons of brain activation for the scene conditions with their respective object conditions. The top row shows the sagittal, coronal, and axial perspectives of a ‘see-through brain’. The bottom row shows activation for the opaque sagittal, coronal, and axial perspectives of the brain. (A): Activations for the episodic memory retrieval network, which include the parahippocampal gyrus, bilateral hippocampi, retrosplenial and posterior parietal cortices, right thalamus, middle temporal cortices, and medial prefrontal cortex. (B): Activations for the network involved in imagining new fictitious experiences, which include the parahippocampal gyrus, right hippocampus, retrosplenial and posterior parietal cortices, and ventromedial prefrontal cortex. (C): Activations for the network involved in recalling previously imagined fictitious experiences, which include the parahippocampal gyrus, right hippocampus, retrosplenial and posterior parietal cortices, and medial prefrontal cortex. From “Using Imagination to Understand the Neural Basis of Episodic Memory” by Hassabis, D., Kumaran, D., & Maguire, E. A., 2007, *The Journal of Neuroscience*, *27*(52), 14365-14374 (https://doi.org/10.1523/JNEUROSCI.4549-07.2007) Copyright 2007 by the Society for Neuroscience

By contrasting the results of the RM, IS, and NS conditions with each of their controls (RO, IO, NO), the network of brain areas responsible for scene construction was also established. The notable areas were the parahippocampal gyrus, hippocampus, retrosplenial cortex, and posterior parietal cortex (Hassabis, 2007b) (see Figure 3).

Figure 3.

Hassabis et al Scene Construction Network



Note. The brain areas activated during the three scene conditions (RM, IS, NS), and therefore likely involved in scene construction, shown using the same perspectives as in Figure 2. The full network includes the parahippocampal gyrus, bilateral hippocampi, retrosplenial and parietal cortices, middle temporal cortices, and medial prefrontal cortex. From "Using Imagination to Understand the Neural Basis of Episodic Memory" by Hassabis, D., Kumaran, D., & Maguire, E. A., 2007, *The Journal of Neuroscience*, *27*(52), 14365-14374 (https://doi.org/10.1523/JNEUROSCI.4549-07.2007) Copyright 2007 by the Society for Neuroscience

This research states that each of these brain areas and the network they encompass all contribute to scene construction by generating and imagining fictitious scenes. This shared function can be attributed to the overlapping brain regions they involve. It is a common observation in neuroscience that brain areas in close proximity with one another often share similar functions. Moreover, the engagement of this network during the recall of both previously imagined and real experiences (RS, IS, NS conditions) suggests that areas within this network are involved in the reconstruction, maintenance, and visualization of complex scenes. The following sections will discuss this network in greater detail.

Parahippocampal Gyrus

The parahippocampal gyrus (PHG) is a brain area involved in episodic memory encoding and retrieval, as well as spatial navigation (Hassabis, 2007b; Epstein, 2008; Sporns, 2013). By contrasting the results of the NS with NO conditions, it as part of a network associated with the creation of newly imagined fictitious scenes (Hassabis, 2007b). Another study also demonstrated that the PHG was involved in scene construction performance (Irish, 2015). These findings suggest that the PHG's spatial navigation function may contribute to scene construction by assisting with the spatial components of a newly created scene, as well as its vividness.

Hippocampus

The hippocampus is located in the temporal lobe and its primary function is memory and spatial associations (Eichenbaum, 1992; Furlan, 2016). The hippocampus being involved in scene construction was demonstrated in a study where patients with hippocampal amnesia were worse at imagining new scenes compared to controlled participants. This study suggests that the hippocampus likely contributes to scene construction by providing the spatial context or environmental setting where the details of a scene are present (Hassabis, 2007a). This incorporates the spatial association function into scene construction.

Retrosplenial Cortex

The retrosplenial cortex (RSC) is located in both the limbic and frontal lobes and is primarily involved in general learning and navigation (Vann, 2009). In addition to these roles, one researcher suggests that the RSC may contribute to scene construction by processing the scene-relevant associations between objects and their contexts (Bar, 2004). One study supports this claim by finding that the RSC was more active while viewing objects strongly associated with a specific context than when it viewed objects weakly associated with a specific context (Bar, 2003). This research also finds that the RSC was active during the three scene conditions (RM, IS, NS) (Hassabis, 2007b). Because the scene conditions likely contain objects within the scene, scene-relevant associations are made for the objects and would explain the RSC's activity during these conditions.

Posterior Parietal Cortex

The posterior parietal cortex (PPC) is situated in the parietal lobe and it is primarily responsible for visual-spatial attention and sensory-motor integration, meaning the process of perceiving motor-related stimuli (Andersen, 2002; Whitlock, 2017). Contrasting the results from the NS and NO conditions, this research suggests that the PPC is involved in the network of constructing new fictitious scenes (Hassabis, 2007b). The PPC may utilize its function of visual-spatial attention during the NS condition. This is because actively constructing and maintaining newly created scenes necessitates focused attention on the visual-spatial components involved.

Episodic Memory

Episodic memory is the memory associated with the recalling of an experience and its details (Pause, 2013). While scene construction is the process of forming the details of a recalled event, episodic memory pertains to the recalling of the event itself. By contrasting the results between the IS and IO conditions, *Hassabis et al* identifies that imagery linked to the recollection of episodic memory activates a network. This network includes the parahippocampal gyrus, right hippocampus, retrosplenial cortex, posterior parietal cortex, precuneus, and posterior cingulate cortex (see Figure 2) (Hassabis, 2007b).

Parahippocampal Gyrus

The episodic memory retrieval function of the parahippocampal gyrus (PHG) holds particular relevance in the context of episodic memory. This function is notably utilized during the 'recall' conditions (RM and RO), both involving the recollection of real autobiographical memories. This utilization arises from the retrieval of already encoded episodic memories that participants were asked to imagine. One study suggests that episodic and autobiographical memory exhibit overlapping brain area activation. The implication is that the PHG may also be involved in autobiographical memory (Gilboa, 2004a).

However, this study also suggests that while episodic and autobiographical memory exhibit overlapping brain area activation, there are distinctions in the activation patterns. For instance, episodic memory activates the right-mid dorsolateral pre-frontal cortex (PFC), a phenomenon not observed in autobiographical memory. Conversely, autobiographical memory activates the ventromedial PFC, which does not occur during episodic memory (Gilboa, 2004a). Given the PHG's role in scene construction through episodic memory retrieval and its activation during autobiographical memory conditions, despite the differing brain area activation between episodic and autobiographical memory, it is likely that the PHG's contribution to autobiographical memory still applies to findings of *Hassabis et al*.

Furthermore, the PHG's involvement in the 'recreate' conditions (IS and IO) is notable. This is because participants were asked to recall a previously created fictitious memory that was newly imagined during the interview session (Hassabis, 2007b). This implies that the PHG is instrumental in the retrieval of both real and fictitious episodic memories.

Right Hippocampus

The right hippocampus is found to be associated with the memory of locations within an environment. Specifically, object location memory and navigating complex spatial environments (Burgess, 20002). The ‘recall’ (RM and RO) and ‘recreate’ (IS, IO) conditions would utilize this function due to participants recalling the events, as opposed to constructing new ones.

However, there is other research suggesting that the right hippocampus is associated with the active short-term memory maintenance of spatial information (Piekema, 2006). This association involving short-term memory is intriguing because it appears to be more applicable to scene construction. While this function may not be utilized during episodic memory, it may be present during scene construction. This is because scene construction involves the bilateral hippocampus, which includes the right hippocampus. This is supported by the right hippocampus being active during the 'imagine' and 'recreate' conditions (Hassabis, 2007b). The bilateral hippocampus may utilize this function of the right hippocampus in the maintenance of scene construction.

Retrosplenial Cortex

Along with its role in the scene construction network, the retrosplenial cortex (RSC) is also a component of the episodic memory network. This is evident through the observed activity of the RSC during the RM and IS conditions (Hassabis, 2007b). One meta-analysis showed that the RSC is consistently active in studies involving autobiographical memory retrieval (Svoboda, 2006). Moreover, other research indicated increased RSC activation during the retrieval of recent autobiographical experiences compared to older ones (Gilboa, 2004b; Woodard, 2007). These findings could explain the RSC's involvement during the RM and IS conditions, where participants were instructed to remember only very recent autobiographical memories (Hassabis, 2007b).

Posterior Parietal Cortex

The posterior parietal cortex (PPC) is another area involved in both scene construction and episodic memory networks. In addition to its involvement with constructing fictitious scenes, the PPC is a part of the network associated with autobiographical memory (Hassabis, 2007b;

Ramanan, 2018; Berryhill, 2010). The PPC's engagement during both fictitious and real memories might be attributed to its functions in visual-spatial attention and sensory-motor integration, as these are likely employed in the processing of both memory types.

Precuneus

The precuneus, located in the parietal lobe, primarily functions in episodic memory retrieval and self-processing operations. These operations involve first-person perspective-taking and the sense of agency (Cavanna, 2006). The precuneus displayed increased activity during the recall of previously imagined episodic-like scenes (Hassabis, 2007b), which may align with its role of episodic memory retrieval. The precuneus is also preferentially engaged during the recall of real memories, which may come from its self-processing operations function. Real memories necessarily adopt a first-person perspective, as that is the only perspective anyone can see without imagination. As a result, given that an aspect of self-processing operations includes processing the environment in a first-person perspective, self-processing would be utilized during the recall of real memories.

Posterior Cingulate Cortex

The posterior cingulate cortex (PCC), situated in the parietal lobe, primarily serves functions related to memory, navigation, narrative comprehension, and internally-directed thought (Leech, 2019; Leech, 2014). Notably, these functions can be involved in autobiographical memory. Autobiographical memory has demonstrated correlations with brain regions associated with episodic memory retrieval (Cabeza 2007; Svoboda 2006). It is possible that this correlation can translate to the 'recall' conditions, the retrieval of autobiographical memories, thus establishing a connection between the functions of the PCC and episodic memory. An additional study has highlighted the involvement of the PCC in episodic memory encoding (Natu, 2019), providing further support for the findings of *Hassabis et al*.

The PPC and precuneus are also preferentially engaged during the recall of real memories (Hassabis, 2007b). This experiment also speculates that the PCC and precuneus play a role in distinguishing real and fictitious memories because of their self-processing and familiarity identification functions (Hassabis, 2007b). Both functions are involved in identifying an individual’s experiences, and that identification may also allow an individual to distinguish real memories from fictitious ones.

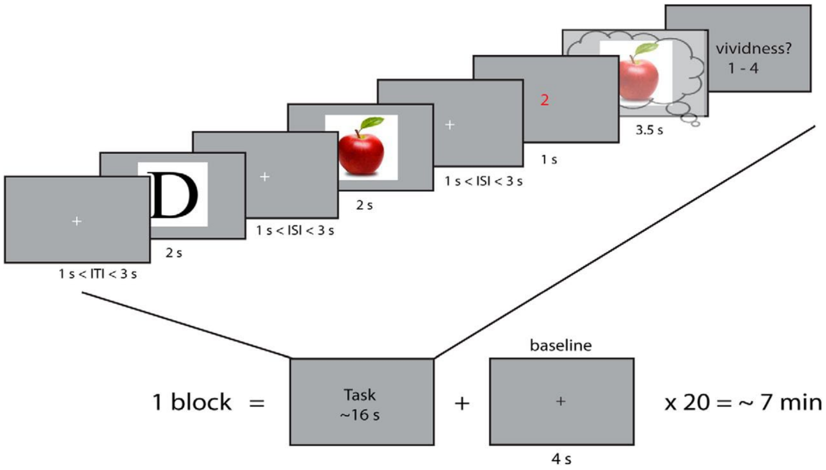
Imagery Vividness

Imagery vividness refers to the clarity, brightness, or intensity of an individual’s imagination as they report it (Marks, 1973). The findings of two studies collectively indicate that imagery vividness triggers activation in the precuneus, insula, early visual cortex (Dijkstra, 2017), parahippocampal gyrus, hippocampus, visual association cortex, and posterior cingulate cortex (Fulford, 2018).

In the study by *Dijkstra et al*, participants first completed the VVIQ and were then presented with pairs of images, which could be two faces, two letters, or two kinds of fruit. Following this, they were instructed to vividly imagine one of the images from each pair. Brain activity was measured using fMRI during this task to assess the imagery vividness experienced during the study (see Figure 4).

Figure 4.

Dijkstra et al Slides



Note. This image illustrates the slides shown during the experimental procedure (left to right). This procedure involved showing participants two objects, belonging to any of the three possible stimulus categories (faces, letters, or fruits). The first object was shown briefly, and then an intermittent period of a few seconds occurred where participants were shown a fixation cross, followed by the second object. After a few seconds, participants were shown another fixation cross, followed by a cue indicating which of the two objects they were supposed to imagine. Afterwards, participants were asked to rate their experienced imagery vividness on a scale of 1 (not vivid at all) to 4 (very vivid). From "Vividness of visual imagery depends on the neural overlap with perception in visual areas" by Dijkstra, N., Bosch, S. E., & van Gerven, M. A. (2017). *Journal of Neuroscience*, *37*(5), 1367-1373. (https://doi.org/10.1523/JNEUROSCI.3022-16.2016)

The VVIQ scores were found to be positively associated with the imagery vividness reported for different stimulus categories (faces, letters, or fruits). Interestingly, the results demonstrated that brain activity during the viewing of letters showed the strongest association with participants' ratings on the VVIQ, followed by fruits, and then faces. This finding provides insights into how specific types of stimuli may influence imagery vividness and its relationship with individual differences in brain activity. The notable active brain areas throughout the experiment were the precuneus, insula, and early visual cortex (Dijkstra, 2017).

Precuneus

The role of the precuneus in imagery vividness is linked to its function in selecting pertinent details during imagery (Ganis, 2004). This function aligns with the finding that the level of detail experienced during imagery significantly impacts judgments of imagery vividness (Dijkstra, 2017). Consequently, the precuneus likely facilitated the participants' ability to experience imagery vividness by filtering and emphasizing the relevant details associated with the specific image category assigned during the study. It is possible that by focusing on these relevant details, the precuneus contributed to the vividness of the mental images generated by the participants.

Insula

The insula, located in the lateral sulcus, primarily functions to process sensory and affective information, and then transmit this processed information to other brain areas (Uddin, 2017; Ardila, 2016). Some research suggests that the insula might play a role in imagery vividness by enabling individuals to imagine from a first-person perspective (Lorey, 2009).

Imagining something necessarily involves adopting a point-of-view, and the first-person perspective represents a viewpoint from the self. In Dijkstra et al, it is possible that participants imagined the images from a first-person perspective as if they were looking at the images themselves. Imagining from a first-person perspective is more probable, as it entails participants envisioning the scenario from their own vantage point, and not from someone viewing them. This would explain how the insula contributes to enhancing imagery vividness, which is by enabling this first-person perspective during visual imagery.

Early Visual Cortex

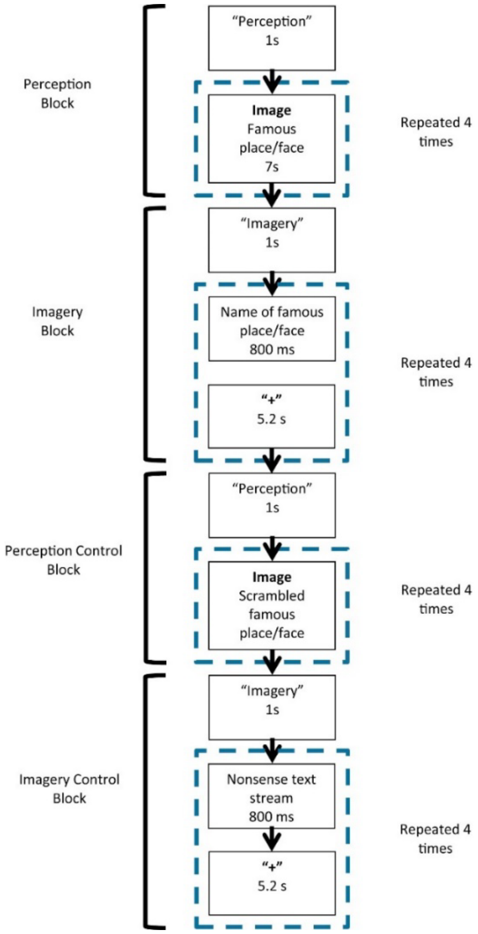
The early visual cortex, located in the frontal lobe, is responsible for the initial stages of visual processing (Albers, 2013). Although it is conceivable that visual processing in this cortex contributes to imagery vividness, a meta-analysis points out that its overall contribution to visual imagery is a subject of debate (Pearson, 2019). This implies that the specific role of the early visual cortex in imagery vividness is also a topic of contention. However, there is also an association of the early visual cortex with processing faces (Dijkstra, 2017), suggesting that its role is related to visual imagery pertaining to faces.

In the experiment by Fulford et al, researchers recruited 15 participants who scored low on the Vividness of Visual Imagery Questionnaire (VVIQ) and 14 who scored high on the measure. The low-scoring group experienced lower imagery vividness, while the high-scoring group experienced higher imagery vividness. Participants were then to participate in four sessions, or blocks: ‘perception’, ‘imagery’, ‘perception control’, and ‘imagery control’.

Participants were presented with black and white images of famous people and places in the' perception' condition. The ‘imagery’ condition presented participants with the names of faces that were presented to them prior, with the intention being that they imagine these. The ‘perception control’ condition had low resolution and inverted versions of the stimuli used in the ‘perception’ condition. The ‘imagery control’ condition presented participants with incoherent letter strings, followed by a request to not imagine anything (Fulford, 2018) (see Figure 5).

Figure 5.

Fulford et al Slides



Note. These are the slides shown during the experimental procedure (top to bottom). Text in quotation marks ("") are the text presented to participants. Text in bold indicates an image that is presented to participants, with a description of the image underneath. Dotted lines specify that a section is repeated more than once, with the number of times repeated being described on the right. The times, in seconds (s), specify the time allotted during each section's presentation. From "The neural correlates of visual imagery vividness–An fMRI study and literature review" by Fulford, J., Milton, F., Salas, D., Smith, A., Simler, A., Winlove, C., & Zeman, A. (2018). *Cortex*, *105*, 26-40. (https://doi.org/10.1016/j.cortex.2017.09.014) Reprinted with permission.

The brain activity of the participants was recorded during the task using fMRI. The researchers also recorded the discrepancies in brain activity between the low-vividness and high-vividness groups. The results demonstrated that the parahippocampal gyrus, hippocampus, posterior cingulate cortex, and visual association cortex were positively associated with imagery vividness (Fulford, 2018).

Parahippocampal Gyrus and Hippocampus

The parahippocampal gyrus (PHG) was active in the low-vividness and high-vividness groups (Fulford, 2018). The PHG being involved in scene construction performance (Irish, 2015), and its activation during this study, suggests that this function may also contribute to imagery vividness. Scene construction performance encompasses the execution of scene construction done by an individual, and imagery vividness is an aspect of this quality. The PHG's activation in both vividness conditions suggests that it plays a role in imagery vividness irrespective of the vividness quality, supporting the findings demonstrating its involvement in the construction of mental scenes and the vividness of those scenes.

The autobiographical memory processing functions of both the PHG and hippocampus may also contribute to the activation of these areas for both groups during the imagery vividness task (Fulford, 2018). Imagining famous people and places may bring up memories of personal experiences. The design involving famous people and places may have triggered participants to utilize autobiographical memory. This is because participants may have had personal experiences relating to these, which means recalling them is recalling an autobiographical memory.

Posterior Cingulate Cortex

The exclusively positive correlation with imagery vividness suggests that the posterior cingulate cortex significantly influences imagery vividness (Fulford, 2018). One plausible reason for this could be its involvement in internally-directed thought.

Internally-directed thought, also referred to as internally-directed cognition, involves how an individual consciously influences the content of their thoughts (Vago, 2022). In this case, participants attempting to vividly imagine something during the experiment is an example of internally directed thought. Thus, the posterior cingulate cortex's involvement in this internally-directed cognitive processes may contribute to imagery vividness.

As previously discussed, memory, in this case associative memory, may also play a role in the relationship between the posterior cingulate cortex and imagery vividness. The interplay of internally-directed thought and memory mechanisms could shed light on the involvement of the posterior cingulate cortex in imagery vividness.

Visual Association Cortex

The visual association cortex encompasses various brain areas within the occipital lobe and is associated with visual processing and associative memory (Gazzaley, 2007; Rosen, 2018). Research suggests that activity in category-preferential visual processing areas within this cortex, meaning they are closely linked to categorical processing, can predict individual differences in memory performance during initial associative memory encoding (Leech, 2014).

Fulford et al involved three conditions imagining several famous people and places that were presented, which were 'perception', 'perception control', and 'imagery'. Given the activation of the visual association cortex during these conditions (Fulford, 2018), this cortex may play a role in recalling these images. Imagining famous individuals and places likely involves associative memory, the ability to recall relationships between concepts (Suzuki, 2005). As a result, participants may have had previous experiences connecting them to these famous individuals or places, employing associative memory to construct and recall these images.

Negative Relationships

This study revealed negative associations with imagery vividness as well. In this case, a negative relationship indicates that activity in these brain areas is associated with lower imagery vividness.

The insula, Area V1, and Area V2 all demonstrated a negative association with imagery vividness (Dijkstra, 2017). Area V1, situated in the occipital lobe, plays a key role in various aspects of visual perception, including object recognition and color perception (McKeeff, 2007; Engel, 1997). Area V2, also located in the occipital lobe, shares similar primary functions to V1. However, V2 goes a step further by processing visual stimuli for additional aspects of visual perception, such as global motion (Furlan, 2016).

In the study, it was discovered that all these brain areas exhibited higher activity during visual imagery tasks in participants with lower imagery vividness scores compared to those with higher scores. One possible explanation is that the brain might struggle to suppress activity from areas that could potentially impede imagery vividness. This idea finds support in the negative association observed between imagery vividness and activity in Area A1 (Dijkstra, 2017).

Area A1, also known as the auditory cortex, is situated in the temporal lobe and is primarily responsible for auditory perception, including aspects such as frequency, pitch, volume, and the motion and spatial location of sounds (Hall, 2003). However, in the context of this study, the task did not require auditory processing, as it solely focused on visual imagery tasks. It is plausible that the activity in Area A1 interfered with the brain areas responsible for visual imagery, contributing to the observed lower imagery vividness.

Another proposed reason is that the brain is compensating for its lower imagery vividness by incorporating more areas of the brain to assist (Dijkstra, 2017). Except for Area A1, all the brain areas seem to contribute to visual imagery in various ways. The brain may be attempting to utilize those areas to increase imagery vividness. Of course, in this research, the compensatory mechanism was not effective in elevating imagery vividness (Dijkstra, 2017).

An additional explanation is provided by the neural efficiency hypothesis, which posits that greater task efficiency typically leads to reduced brain activation. This is supported by the results where participants with higher imagery vividness scores displayed overall reduced brain activation, with fewer total brain areas being engaged. These findings match up with the fact that, among participants who scored low in imagery vividness, these four brain areas, all located in the frontal region, were preferentially engaged (Dijkstra, 2017).

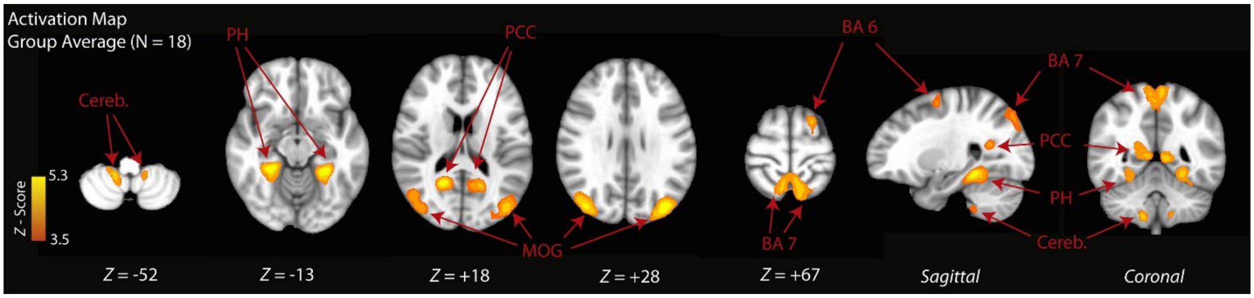
Visuospatial Imagery

Visuospatial processing is the ability to observe, manipulate, and transform visual images (Dehn, 2011). Visuospatial processing involves the use of visuospatial stimuli, and visuospatial stimuli are present in visuospatial imagery as well. As a result, the definition of visuospatial processing will also be used for visuospatial imagery.

In a study by *Whittingstall et al*, participants were instructed to silently perform Roland's Hometown Walking Task (RHWT), a mental spatial navigation task through a familiar environment (Roland, 1987). The task required participants to navigate following their most familiar route. Employing both dMRI and fMRI techniques, the study revealed increased activity in the parahippocampal gyrus, precuneus, and posterior cingulate cortex during this task, implicating them in a visuospatial imagery network (Whittingstall, 2014) (see Figure 6).

Figure 6.

Whittingstall et al Visuospatial Imagery Network



Note. The average brain activation across all participants, indicated by the Z-scores which are used to denote the strength of activation. The images are axial-perspective image slices of the brain taken during the brain imaging process. The coordinates of these are displayed below the axial-perspective image slices as “Z =”. These image slices reveal that the network for visuospatial imagery (left to right) involves the cerebellum, parahippocampal gyrus (labelled as PH), posterior cingulate cortex (PCC), middle occipital lobe (labelled as MOG, or middle occipital gyrus), precuneus (BA 7), and frontal area BA 6 (BA 6). This image was cropped from its original version to keep material strictly related to brain area activation. Adapted from “Structural network underlying visuospatial imagery in humans” by Whittingstall, K., Bernier, M., Houde, J. C., Fortin, D., & Descoteaux, M. (2014). *Cortex*, *56*, 85-98. (https://doi.org/10.1016/j.cortex.2013.02.004) Adapted with permission.

Parahippocampal Gyrus

Compared to other brain areas, the parahippocampal gyrus (PHG) showed the most significant activation during the RHWT. This activation is likely attributed to the task's demand for retrieving familiar spatial knowledge (Whittingstall, 2017). This notion aligns with previous research demonstrating PHG activity during tasks specifically centered around route imagery (Sharma, 2016; Shelton, 2002). Furthermore, other research finds the PHG to be active during the learning of virtual environments with personally significant landmarks, and inactive during the learning of virtual environments with no landmarks (Maguire, 1998). In this study, learning involved the exploration of these environments, which implies the participants were following a route. This exclusive activation suggests that the PHG may be involved in the learning of familiar route-like environments.

Precuneus and Posterior Cingulate Cortex

The results show that both the precuneus and the posterior cingulate cortex (PCC) were highly connected with other brain areas during the RHWT (Whittingstall, 2017). Specifically, the structural connections originating from the occipital, parietal, and temporal lobes and passing through the precuneus linked these lobes to the frontal lobe. On the other hand, the PCC connected the three former lobes with each other. These intricate connections highlight the PCC and precuneus as significant hubs facilitating the interplay between ventral and dorsal processing of visuospatial memory (Whittingstall, 2017).

Negative Associations

Results also showed a consistent and moderate deactivation in Areas V1 and V2 (calcarine gyrus). These findings align with a meta-analysis of PET studies, which observed that spatial imagery tasks result in a deactivation of the early visual cortex, which contains the calcarine gyrus (Mazard, 2004). Moreover, there was consistent connectivity demonstrated between the deactivated calcarine gyrus and the activated posterior cingulate cortex (PCC) and middle occipital gyrus (MOG). This suggests that the activity in the calcarine gyrus may be influenced by feedback from higher cortical areas, such as the latter two (Whittingstall, 2017).

Discussion and Conclusions

The research discussed in this review suggests that specific brain regions are associated with the identified subcategories of visual imagery. However, there are several limitations of the present review that likely impacted the findings. In terms of methodology, there were limited keywords and databases used, resulting in research that does not completely reflect the entire body of literature on visual imagery.

For example, this review found that Area V1 is negatively associated with both imagery vividness and visuospatial imagery. While this suggests that Area V1 does not contribute to visual imagery, one literature review suggests that it does contribute to it in some visual imagery research and does not in others (Kosslyn, 2003). Similarly, the insula was found to have displayed both a positive and negative association with imagery vividness, suggesting dissimilar findings between the two research projects discussed (Dijkstra, 2017; Fulford, 2018). Both nuances could be explored in future research.

While this research aimed to present an overview of different visual imagery subcategories and to distinguish the contributions of involving brain areas, some visual imagery topics were not covered. The scope of this project was limited to four visual imagery subcategories, but there are additional ones that can be explored. Some examples include motor imagery (Iseki 2008; Munzert, 2009a; McAvinue, 2008; Neuper, 2005; Munzert, 2009b), visual imagery involving emotional stimuli (Kosslyn, 2001; Suess, 2015; Gollnisch, 1993; Vianna, 2009; Holmes, 2005), or visual imagery involving specific stimuli, such as the briefly mentioned fruits, faces, and letters (Fulford, 2018; Ishai, 2002; O'Craven, 200). There is also potential to explore more qualities of the brain and their associations with visual imagery, such as brain area size (Bergmann, 2015) and pathways.

Regarding pathways, there is an ongoing debate in the literature over the extent to which visual imagery pathways overlap with perception pathways (Kosslyn, 2001; Bartolomeo, 2008; Gardini, 2009, Dentico, 2014). Perhaps future research in the same vein could investigate this overlap and its relation to the pathways of various visual imagery subcategories. This could provide stronger insight into the debate.

The research by Winlove et al is a project that must be acknowledged, as it is a large-scale coordinate-based meta-analysis of visual imagery incorporating 40 research projects. It determined the neural origins of visual imagery by utilizing the Activation Likelihood Estimation (ALE) algorithm, which allows for the calculation of active areas utilizing the findings of visual imagery research (Winlove, 2018). This is similar to the research done here in that it attempts to highlight the prominent areas involved in visual imagery. However, there are limitations to using the ALE algorithm for visual imagery research. Notably, it does not differentiate brain activity based on task (Winlove, 2018). As a result, the potential distinction that could be made with different visual imagery subcategories is lost. A meta-analysis utilizing this method but making separate ALE calculations for different subcategories could offset this limitation.

This literature review contributes to the research on visual imagery by providing a succinct discussion of brain areas involved in visual imagery, and their contributions to different visual imagery subcategories. This discussion is necessary due to how the current literature on visual imagery lacks an overarching investigation into how the brain areas involved in visual imagery contribute to these various subcategories. Future research focusing on this may reveal greater comprehensive insights into visual imagery.

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